

REPRODUCTIVE CHARACTER DISPLACEMENT IN *Lymantria monacha* FROM NORTHERN JAPAN?⁵

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Abstract—Our objective was to test the hypothesis that the pheromone blend and/or diel periodicity of pheromonal communication differ in populations of the nun moth, *Lymantria monacha* (Lepidoptera: Lymantriidae), from eastern Asia (northern Honshu, Japan) and Central Europe (Bohemia, Czech Republic). Coupled gas chromatographic–electroantennographic detection (GC-EAD) analyses of pheromone gland extract of female *L. monacha* from Japan confirmed the presence of compounds previously identified in pheromone extracts of *L. monacha* from Bohemia, as follows: (Z)-7-octadecene, 2-methyl-(Z)-7-octadecene (2me-Z7-18Hy), *cis*-7,8-epoxy-octadecane (monachalure), and *cis*-7,8-epoxy-2-methyloctadecane (disparlure). Field experiments in Honshu suggested that (+)-monachalure is the major pheromone component of *L. monacha*. 2me-Z7-18Hy significantly enhanced attractiveness of (+)-monachalure. Addition of (+)-disparlure to (+)-monachalure plus 2me-Z7-18Hy in Honshu and Bohemia increased attractiveness of lures by 1.2 and 20 times, respectively, indicating that (+)-disparlure is of least and most significance in the respective *L. monacha* populations. Moreover, capture of male *L. monacha* in pheromone-baited traps between 18:00 and 24:00 hr in Bohemia and 2:00 and 5:00 hr in Honshu revealed a markedly different diel periodicity of pheromonal communication. Pheromonal communication late at night and use of (+)-monachalure, rather

⁵Dedicated to Dr. Hans-Karl Dettmar in honor of his 73rd birthday.

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than (+)-disparlure, as the major pheromone component by *L. monacha* in Honshu may have resulted from interspecific competition with coseasonal *L. fumida*, which uses the early night for pheromonal communication and (+)-disparlure as major pheromone component. Whether communication channel divergence of *L. monacha* in Honshu indeed constitutes a case of reproductive character displacement is difficult to prove. The evolution of such divergence in *sympatric* populations of *L. fumida* and *L. monacha* would have to be demonstrated.

Key Words—*Lymantria monacha*, *Lymantria fumida*, *Lymantria dispar*, diel periodicity, interspecific competition, reproductive character displacement, strain, (7*R*, 8*S*)-*cis*-7,8-epoxy-2-methyloctadecane, (+)-disparlure, (7*R*, 8*S*)-*cis*-7,8-epoxy-octadecane, (+)-monachalure, 2-methyl-(*Z*)-7-octadecene, (*Z*)-7-octadecene.

INTRODUCTION

The nun moth, *Lymantria monacha* (Lepidoptera: Lymantriidae), is a significant forest defoliator. Polyphagous caterpillars defoliate gymnosperm trees mainly in the genera *Picea* (spruce), *Pinus* (pine), *Larix* (larch), and *Abies* (fir), but also feed on angiosperm trees, including *Fagus* (beech), *Carpinus* (white beech), *Betula* (birch), and *Quercus* (oak) spp. (Wellenstein, 1978).

The first recorded *L. monacha* population outbreak (1853–1864) occurred in European Russia. In this outbreak, 147,000,000 m³ of timber were killed (Bejer, 1988). Since then, outbreaks have occurred throughout Europe. Five outbreaks are recorded in Poland between 1946 and 1986 (Sliwa and Sierpinski, 1986). During the largest, from 1978 to 1983, over 2 million ha of spruce, pine, and larch forests (one quarter of Poland's forests) were infested and partly defoliated (Schönherr, 1985).

In Europe and western Asia, the northern border of the *L. monacha* range coincides with the September isotherm of 10.5°C, which extends from the southern part of England and Scandinavia to the Ural Mountains (Wellenstein, 1978; Bejer, 1988). The southern extent of its range coincides with the isotherm of >20°C for June, July, and August. This isotherm line crosses central Spain, Corsica, Italy, the Adriatic coast from Slovenia to northern Greece and the Black Sea. The range of *L. monacha* extends, disjunctly, eastward into eastern China, Korea and Japan. Asian populations consist of white color morphs with black spotting. Melanistic forms, as frequently found in Europe (Keena et al., 1998), are absent.

Pheromone blend and diel periodicity of pheromonal communication in *L. monacha* from Central Europe and Japan could differ, because respective populations: (1) occupy different geographic ranges, (2) are reproductively isolated, and (3) are part of lymantriid communities that contrast in numbers of congeners. For example, the July–August lymantriid community of Honshu (northern Japan) comprises *L. monacha*, gypsy moth, *L. dispar*, pink gypsy moth, *L. mathura*, *L. fumida*, *L. lucescens*, and *L. bantaizana*. Presence (Honshu) or absence

(Bohemia, Czech Republic) of *L. mathura*, *L. fumida*, *L. lucescens*, and *L. bantiana* could conceivably affect interspecific competition for communication channels, and thus pheromonal communication in *L. monacha*.

Pheromonal communication of *L. monacha* in Bohemia is mediated by a complex volatile blend. At a 10 : 10 : 1 ratio, the three pheromone components (7*R*, 8*S*)-*cis*-7,8-epoxy-2-methyloctadecane [(+)-disparlure] (Bierl et al., 1975; Klimetzek et al., 1976), (7*R*, 8*S*)-*cis*-7,8-epoxy-octadecane [(+)-monachalure] (Gries et al., 1996), and 2-methyl-(*Z*)-7-octadecene (2me-*Z*7-18Hy) (Grant et al., 1996; Gries et al., 1996), synergistically attract male *L. monacha*, whereas (–)-disparlure, (+)- and (–)-monachalure, 2me-*Z*7-18Hy, and (*Z*)-7-octadecene (*Z*7-18Hy) synergistically prevent cross-attraction of male *L. dispar* (Gries et al., 1996).

This study reports contrasting pheromone blends and diel periodicities of pheromonal communication in two geographically remote populations of *L. monacha*, and suggests reproductive character displacement as a mechanism responsible for these differences.

METHODS AND MATERIALS

Experimental Insects and Chemical Analyses. Pupae of *L. monacha* were collected in northern Japan. Abdominal tips with pheromone glands of calling, virgin female moths were removed and placed in redistilled hexane. These extracts were hand-carried, and light-trapped male moths couriered to Simon Fraser University in Canada. Aliquots of one female equivalent (FE) of pheromone gland extract and authentic standards were analyzed by coupled gas chromatographic–electroantennographic detection (GC-EAD) (Arn et al., 1975), using a Hewlett Packard (HP) 5890A gas chromatograph equipped with a fused silica column (30 m × 0.25 or 0.32 mm ID) coated with either DB-210, DB-5, or DB-23 (J&W Scientific, Folsom, California). Synthetic chemicals for laboratory and field testing, including (+)- and (–)-disparlure, (+)- and (–)-monachalure, 2-methyl-(*Z*)-7-octadecene (2me-*Z*7-18Hy), and (*Z*)-7-octadecene (*Z*7-18Hy), were available from previous work (Gries et al., 1996). If indicated, compounds were purified (>95%) by high-performance liquid chromatography (HPLC), employing a Waters LC 626 high-performance liquid chromatograph equipped with a Waters 486 variable wavelength UV visible detector, a Waters 746 data module, and a Nova-Pak C₁₈ column (3.9 × 300 mm) with 1 ml/min of acetonitrile flow.

Composition of Pheromone Blends. All field experiments employed a complete randomized block design with 9–12 blocks (replicates) each. Experiments were conducted in forests near (<50 km) the cities of Morioka (Honshu) and Zbraslav (Bohemia). Forests were stocked mainly with Japanese larch, *Larix leptolepsis*, and Norway spruce, *Picea abies*, respectively. Delta-like traps were made from 2-liter milk cartons (Gray et al., 1984), coated with Tanglefoot (The

Tanglefoot Company, Grand Rapids, Michigan), and suspended from trees 1.5 m above ground at 15 to 20-m spacing. They were baited with a gray sleeve stopper (identification # 10600275; West Pharmaceutical Services, Lionville, Pennsylvania) impregnated with candidate pheromone components in HPLC-grade hexane.

Experiment 1 compared attraction of male *L. dispar* and *L. monacha* to (+)-disparlure and (+)-monachalure, respectively. With only (+)-monachalure significantly attractive to male *L. monacha* (and thus likely being the major pheromone component of *L. monacha* in Honshu), experiments 2–3 investigated potential synergists, including (+)-disparlure, 2me-Z7–18Hy (the hydrocarbon analog of disparlure), and Z7–18Hy (the hydrocarbon analog of monachalure). Experiments 4–6 tested the effect of presence and proportion of (+)-monachalure in pheromone blends on attraction of male *L. monacha*, *L. fumida*, and *L. dispar*. Experiments 7–10 compared the relative importance of (+)-disparlure in pheromone blends for attraction of male *L. monacha* in Honshu and Bohemia.

Various treatments in several experiments did not attract any male moths. Despite transformation, trap catch data were not normally distributed and were thus analyzed by nonparametric analyses of variance (Friedman's test) followed by comparison of means by Bonferroni (Dunn) *t* test (Zar, 1984; SAS/STAT, 1988). In all analyses, $\alpha = 0.05$.

Diel Periodicity of Pheromonal Communication. Diel periodicities of pheromonal communication of *L. monacha* in Bohemia (experiment 10) and of *L. monacha* and *L. fumida* in Honshu (experiment 11) were assessed by hourly recording captures of male moths in pheromone-baited traps. Experiment 10 had already been conducted during nine nights in 1989 and employed two sticky beta type traps (ÚOCHB AVCR, Praha, Czech Republic) baited with rubber septa impregnated with (\pm)-disparlure (100 μ g) (ÚOCHB AVCR). For experiment 11, the 20 sticky Delta traps (see above) were suspended from trees ~ 2 m above ground at 15 to 20-m intervals. Traps were baited with gray sleeve stoppers impregnated with the three-component blend of (+)-monachalure (50 μ g), (+)-disparlure (5 μ g), and 2me-Z7–18Hy (5 μ g) for male *L. monacha* or with the two-component blend of (+)-disparlure (50 μ g) and 2me-Z7–18Hy (5 μ g) for male *L. fumida* (Schaefer et al., 1999). Baits for *L. monacha* and *L. fumida* were alternated between traps.

RESULTS

Comparative GC-EAD analyses of pheromone gland extract and synthetic standards on three fused silica columns confirmed the presence of Z7–18Hy (peak 1), 2me-Z7–18Hy (peak 2), monachalure (peak 3) and disparlure (peak 4) in pheromone extracts of female moths (Figure 1). Disparlure appeared to be most

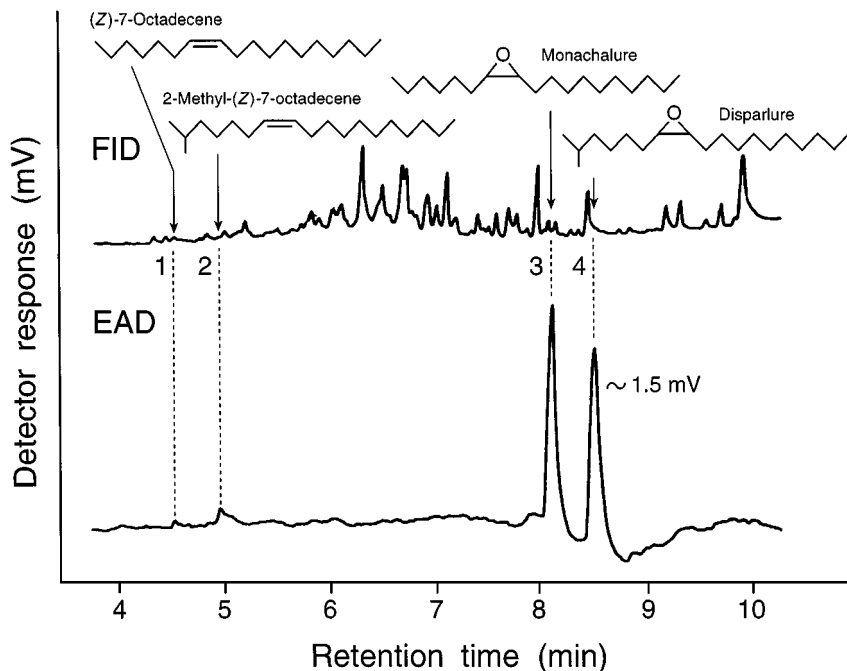


FIG. 1. Flame ionization detector (FID) and electroantennographic detector (EAD: male *L. monacha* antenna) responses to one female (*L. monacha* from Honshu) equivalent of pheromone gland extract. A gas chromatograph was fitted with a fused silica column (30 m \times 0.25 mm ID) coated with DB-23; temperature program: 50°C (1 min), then 25°C/min to 100°C then 10°C/min to 220°C (10 min). Compound abbreviations: **1** = (*Z*)-7-octadecene (*Z*7-18Hy); **2** = 2-methyl-(*Z*)-7-octadecene (2me-*Z*7-18Hy); **3** = (*7R,8S*)-*cis*-7,8-epoxy-octadecane [(+)-monachalure] or (*7S,8R*)-*cis*-7,8-epoxy-octadecane [(-)-monachalure]; **4** = (*7R,8S*)-*cis*-7,8-epoxy-2-methyloctadecane [(+)-disparlure] or (*7S,8R*)-*cis*-7,8-epoxy-2-methyloctadecane [(-)-disparlure]. Retention indices: *Z*7-18Hy: 1782 (DB-5), 1792 (DB-210), 1825 (DB-23); 2me-*Z*7-18Hy: 1842 (DB-5), 1860 (DB-210), 1877 (DB-23); monachalure: 1971 (DB-5), 2234 (DB-210), 2284 (DB-23); disparlure: 2032 (DB-5), 2306 (DB-210), 2339 (DB-23).

abundant, but GC-mass spectrometry (MS) confirmed that another quantitatively significant compound co-eluted with it. All four EAD-active components occurred at quantities too low to reliably calculate their relative proportion.

In field experiment 1, (+)-monachalure attracted male *L. monacha*, whereas (+)-disparlure attracted male *L. dispar* (Figure 2). The hydrocarbon analog of disparlure, 2me-*Z*7-18Hy, was significantly more effective than (+)-disparlure in enhancing attractiveness of (+)-monachalure (Figure 2, experiment 2). In contrast,

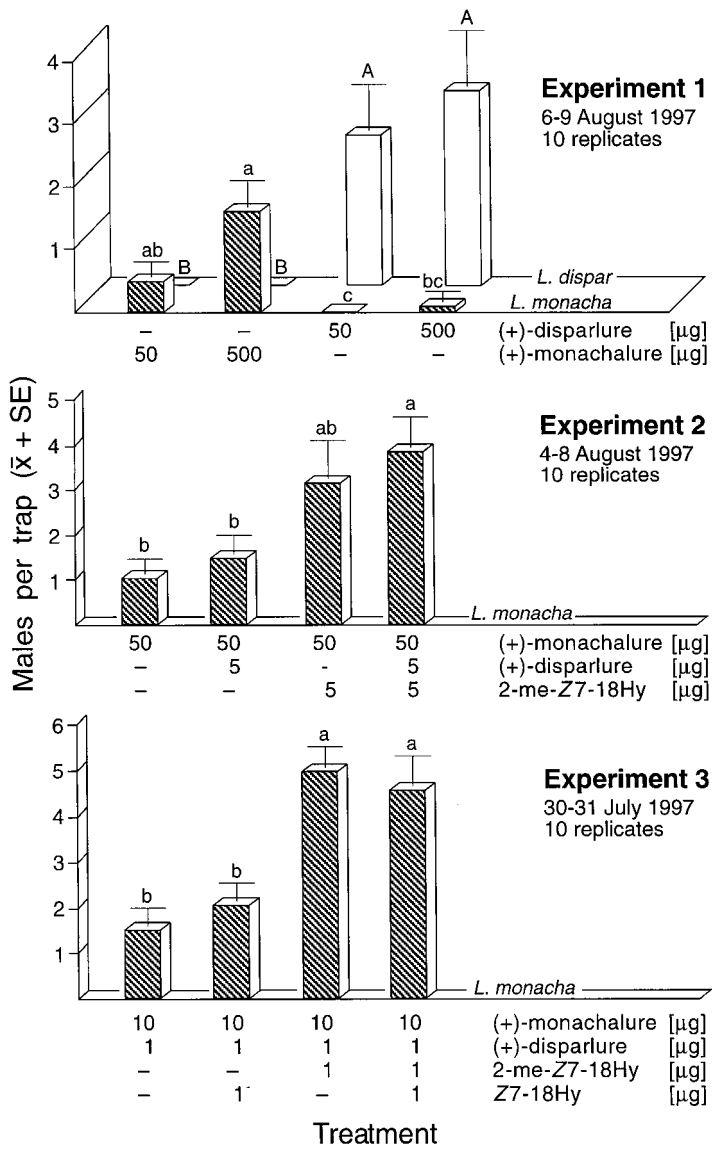


FIG. 2. Mean number of male *L. monacha* or *L. dispar* captured in sticky Delta traps baited with various volatile blends; larch forests near the city of Morioka (northern Honshu, Japan). Compound abbreviations as in Figure 1. Bars within rows of each experiment with the same letter superscript are not significantly different; nonparametric analysis of variance by ranks (Friedman's test) followed by comparison of means [Bonferroni (Dunn) *t* test, *P* < 0.05] (Zar, 1984; SAS/STAT, 1988).

the hydrocarbon analog of monachalure, Z7-18Hy, had no behavioral activity (Figure 2, experiment 3). A low proportion of (+)-monachalure in three-component blends resulted in hardly any captures of males (Figure 3, experiment 4). Conversely, addition of (+)-monachalure at increasing quantities to the two-component blend of (+)-disparlure and 2me-Z7-18Hy significantly enhanced trap captures of male *L. monacha*, whereas captures of male *L. fumida* were not affected (Figure 3, experiment 5). Similarly, addition of (+)-monachalure (10 μ g) to a blend of (+)-disparlure (10 μ g) and 2me-Z7-18Hy (1 μ g) significantly increased captures of male *L. monacha*, failed to affect captures of *L. fumida*, and suppressed captures of male *L. dispar* (Figure 3, experiment 6). The same three-component blend but with (+)-disparlure at 1 μ g attracted only male *L. monacha* (Figure 3, experiment 6). (+)-Disparlure at 5 or 50 μ g, but not 500 μ g, in admixture with (+)-monachalure (50 μ g) and 2me-Z7-18Hy (5 μ g) doubled trap captures of male *L. monacha* in Honshu (Figure 4, experiments 7 and 8). In Bohemia, addition of 5 and 50 μ g of (+)-disparlure to pheromone baits of an equivalent experiment increased trap captures of male *L. monacha* by 10 and 20 times, respectively (Figure 4, experiment 9).

Male *L. monacha* in Bohemia and Honshu were captured in pheromone-baited traps from 19:00 to 24:00 hr and 02:00 to 05:00 hr, respectively (Figure 5).

DISCUSSION

Evidence for Different Strains of L. monacha. Our data support the hypothesis that there are different strains of *L. monacha*. The possibility that we studied different species—rather than strains—was excluded based on comparisons of genitalia (P.W.S., unpublished data) from specimens collected in Honshu and Bohemia. Female *L. monacha* from both strains employ pheromone blends with the same three components but of different relative importance. Moreover, trap captures of males between 19:00 and 24:00 hr in Bohemia and between 02:00 and 05:00 hr in Honshu reflect a marked difference in diel periodicity of pheromonal communication.

In Honshu, (+)-monachalure is the major pheromone component of *L. monacha*. It was more attractive to males than (+)-disparlure (Figure 2, experiment 1), and pheromone blends with no or little (+)-monachalure failed to attract significant numbers of males (Figure 3). The fact that (+)-monachalure suppressed cross-attraction of male *L. dispar* (Figure 3, experiment 6) is supportive evidence that (+)-monachalure is the major component in the *L. monacha* pheromone. Synergistic activity expressed by 2me-Z7-18Hy exceeded that of (+)-disparlure (Figure 2, experiment 2), suggesting that the hydrocarbon analog of disparlure is the second most important pheromone component. (+)-Disparlure as

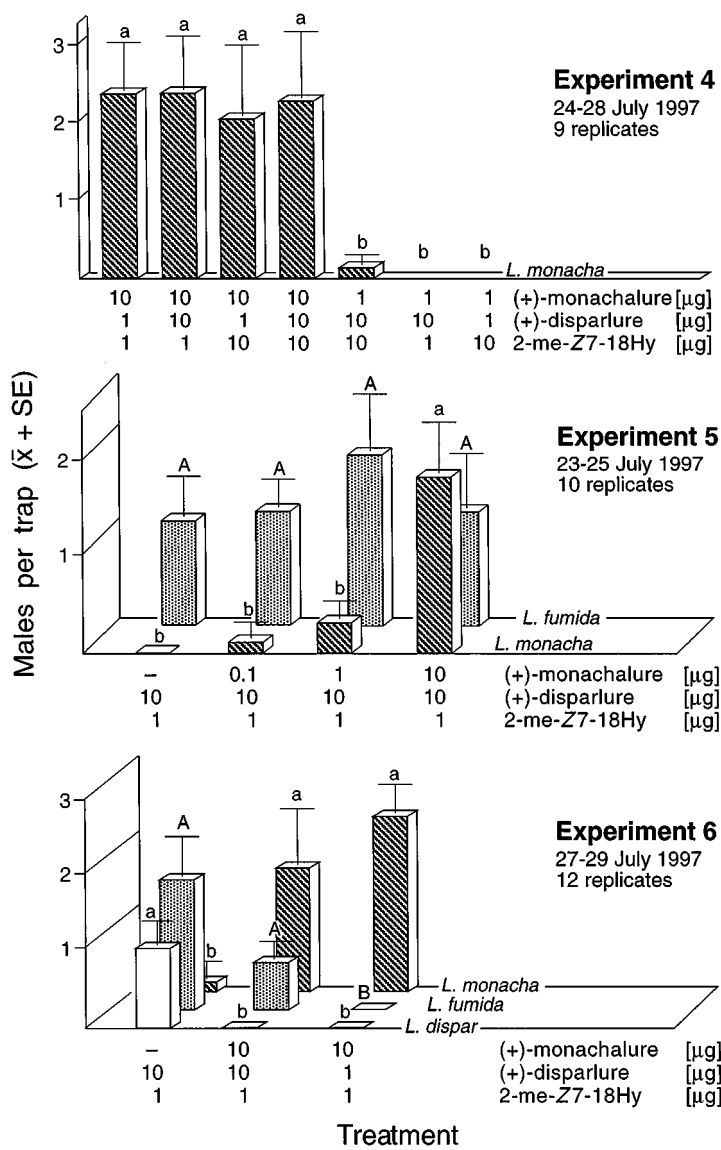


FIG. 3. Mean number of male *L. monacha*, *L. fumida*, or *L. dispar* captured in sticky Delta traps baited with various volatile blends; larch forests near the city of Morioka (northern Honshu, Japan). Compound abbreviations as in Figure 1. Bars within rows of each experiment with the same letter superscript are not significantly different; nonparametric analysis of variance by ranks (Friedman's test) followed by comparison of means [Bonferroni (Dunn) *t* test, $P < 0.05$] (Zar, 1984; SAS/STAT, 1988).

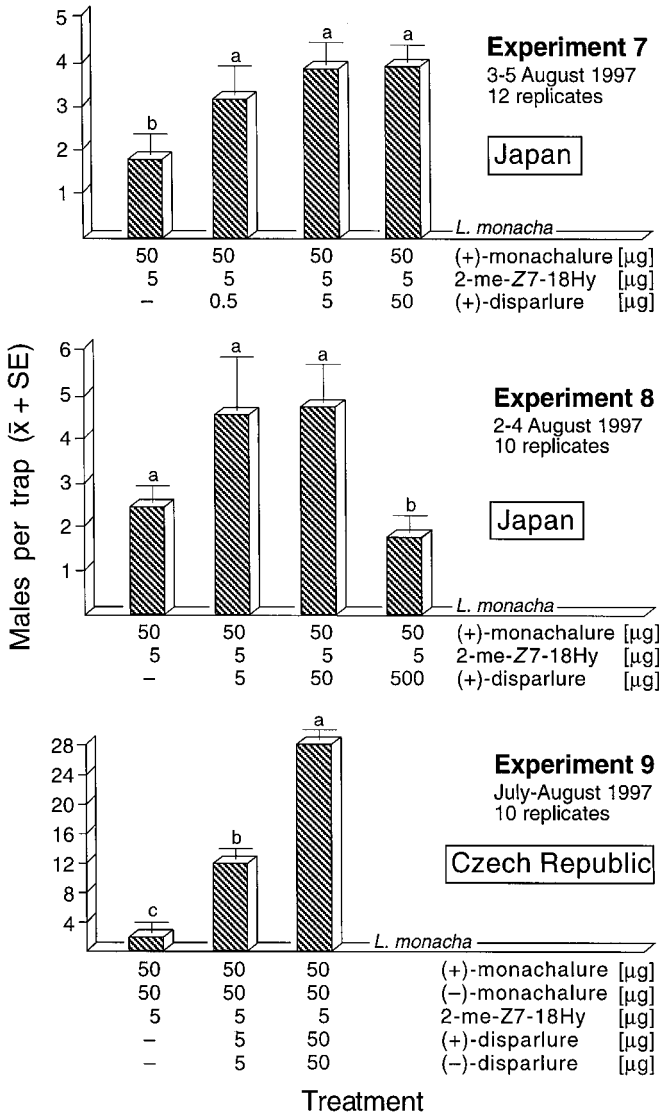


FIG. 4. Mean number of male *L. monacha* captured in sticky Delta traps baited with various volatile blends; larch forests near the city of Morioka (northern Honshu, Japan) (experiments 7 and 8) and spruce forests near the city of Zbraslav (Czech Republic) (experiment 9). Compound abbreviations as in Figure 1. Bars with the same letter superscript in each experiment are not significantly different; nonparametric analysis of variance by ranks (Friedman's test) followed by comparison of means [Bonferroni (Dunn) t test, $P < 0.05$] (Zar, 1984; SAS/STAT, 1988).

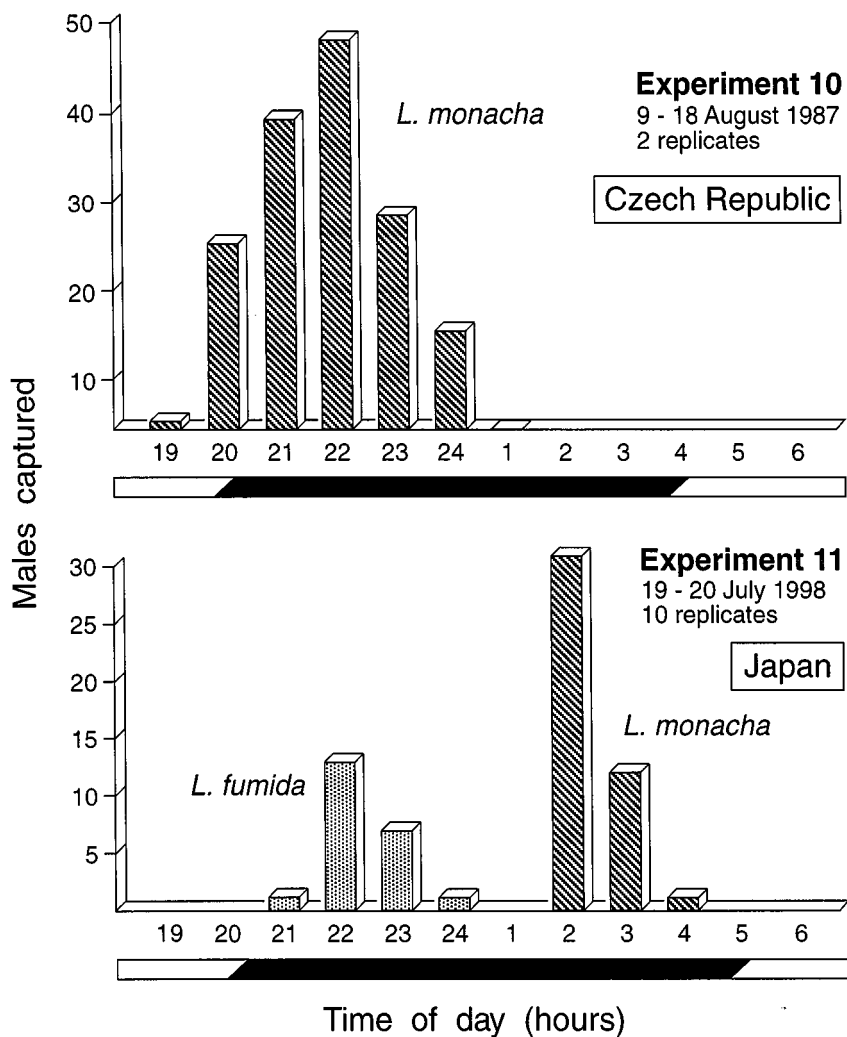


FIG. 5. *Top*: Total numbers of male *L. monacha* captured in sticky Beta traps baited with (\pm)-disparlure ($100\ \mu\text{g}$). Spruce forests near the city of Zbraslav (Czech Republic). *Bottom* (adapted from Schaefer et al., 1999): Total numbers of male *L. monacha* and *L. fumida* captured in 20 sticky Delta traps baited with (+)-monachalure ($50\ \mu\text{g}$), (+)-disparlure ($5\ \mu\text{g}$), and 2me-Z7-18Hy ($5\ \mu\text{g}$) for male *L. monacha* or with (+)-disparlure ($50\ \mu\text{g}$) and 2me-Z7-18Hy ($5\ \mu\text{g}$) for male *L. fumida*. Larch forests near the city of Morioka (northern Honshu, Japan). Black horizontal bars indicate scotophase.

a third pheromone component has only weak behavioral activity. Added to a binary blend of (+)-monachalure and 2me-Z7-18Hy, it barely increased (Figure 2, experiment 2) or doubled (Figure 4, experiments 7 and 8) attractiveness of the lure. This marginal effect of (+)-disparlure in the pheromone blend of *L. monacha* from Honshu contrasts with superior importance of (+)-disparlure in the pheromone blend of *L. monacha* from Bohemia. In Bohemia, addition of (+)-disparlure at 5 and 50 μg to the pheromone blend increased captures of males by 10 and 20 times, respectively (Figure 4, experiment 9).

There was no significant difference in antennal response pattern in GC-EAD analyses of pheromone extract of female *L. monacha* from Honshu (Figure 1) and Bohemia (Gries et al., 1996). This result does not reflect the contrasting importance of (+)-monachalure and (+)-disparlure in pheromone blends of the two strains, supporting our contention that GC-EAD analyses help determine the presence but not behavioral significance of (candidate) pheromone components.

With (+)-monachalure and (+)-disparlure being the major pheromone component of *L. monacha* in Honshu and Bohemia, respectively, the question remains whether pheromone-based detection surveys for *L. monacha* in North America ought to deploy strain-specific pheromone lures. The three-component blend of (+)-disparlure, (+)-monachalure and 2me-Z7-18Hy at a 10 : 10 : 1 ratio was most attractive to males in Bohemia (Gries et al., 1996). The same blend and blend ratio is effective in attracting males in Honshu (Figure 3, experiment 4), although the amount of (+)-disparlure could be reduced 10-fold without any effect. The presence of (–)-disparlure and (–)-monachalure had no effect on attraction of males in Bohemia (Gries et al., 1996) or Honshu (data not shown). Thus, the recently developed pheromone lure for *L. monacha* detection surveys in North America (Morewood et al., 1999), containing (±)-disparlure, (±)-monachalure and 2me-Z7-18Hy at a 20 : 20 : 1 blend remains suitable for attraction of *L. monacha* from both Central Europe and Japan (Gries et al., 1998).

Reproductive Character Displacement in L. monacha Strain from Japan?

There are numerous local populations of *L. monacha* with geno- and phenotypic characteristics shaped by physical and biological factors of the local environment. If we consider the presence of congeners a biological factor (Linn and Roelofs, 1995), five congeners (*L. dispar*, *L. fumida*, *L. mathura*, *L. lucescens*, and *L. bantaizana*) in Honshu should constitute a greater “factor” than the single congener (*L. dispar*) in Bohemia. With five synchronic congeners emitting communication signals, the forest habitat certainly becomes noisy, with selection pressure to improve the signal-to-noise ratio of communication channels (Baker, 1985; Cardé and Baker, 1984). Competition-induced reproductive character displacement *sensu* Butlin (1987) (divergence of traits that are coincidentally shared by sympatric species after speciation has occurred, so that hybridization is impossible) may cause signal divergence to avoid heterospecific matings. We hypothesize that dissimilar communication channels of *L. monacha* in Bohemia and Honshu

are the result of signal divergence caused by *L. fumida* as a competing species in Honshu.

According to our hypothesis, *L. fumida* seem to have affected both communication time and signal (pheromone blend) of *L. monacha*. With *L. fumida* signaling early at night, signaling of *L. monacha* has shifted to the early morning (Figure 5). With (+)-disparlure being most important in the pheromone of *L. fumida* (Schaefer et al., 1999), it has become insignificant in the pheromone of *L. monacha* (Figure 2, experiment 2; Figure 4, experiments 7 and 8). Our hypothesis that *L. monacha* in Honshu has substituted (+)-disparlure with (+)-monachalure as its major pheromone component (in response to competing *L. fumida*) is supported by the fact that the hydrocarbon analog of monachalure (Z7-18Hy) has no behavioural activity (Figure 2; experiment 3), whereas the hydrocarbon analog of disparlure (2me-Z7-18Hy) remains a synergistic pheromone component (Figure 2, experiments 2 and 3).

The concept of reproductive character displacement was proposed by Löfstedt et al. (1991) to explain pheromone variation in closely related ermine moths and can be considered in the context of studies that demonstrate geographic differences in a species' pheromone in the presence of competing species. For example, male *Archips argyrospilus* from New York respond to a more narrowly defined blend of pheromone components than do conspecifics from British Columbia, likely due to interference by the sibling species *A. mortuanus* in New York (Cardé et al., 1977; Butlin., 1995). Similarly, contrasting pheromone blends of the oblique-banded leafroller, *Choristoneura rosaceana* from New York (Hill and Roelofs, 1979) and British Columbia (Vakenti et al., 1988) may be attributable to the competing species *Archips rosanus* in British Columbia (Thomson et al., 1991). Finally, saturniid female and male *Hemileuca electra mojavensis* may have modified their pheromone-based communication to minimize interference from congeneric *H. burnsi* (McElfresh and Millar, 1999).

The above-cited examples and our own data favor the hypothesis that interspecific competition *can* be a selective force on a species' communication channel. Whether communication channel divergence of *L. monacha* in Honshu indeed constitutes a case of reproductive character displacement is difficult to prove. The evolution of such divergence in *sympatric* populations of *L. fumida* and *L. monacha* would have to be demonstrated. Greater differences, if demonstrated, in communication channels of *L. fumida* and *L. monacha* in *sympatric* than in *allopatric* populations in eastern Asia would support our hypothesis that the pheromone biology of *L. monacha* was shaped, in part, by competition with *L. fumida*.

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